



Effects of global warming on the potential distribution ranges of six *Quercus* species (Fagaceae)

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ABSTRACT

The impacts of global warming on the spatial extent and location of suitable habitat can be examined through spatially explicit projections of climatic niches. We modeled the climatic niche of six oaks (*Q. agrifolia*, *Q. cedrosensis*, *Q. chrysolepis*, *Q. devia*, *Q. palmeri* and *Q. peninsularis*), some rare and others widely distributed, occurring within the Baja California Peninsula, Mexico, and projected future distributions under two contrasting scenarios of global warming. We also estimated the breadth of the climatic niche of each species and associated it with current and future distributions. We found that climate warming will modify the distribution of suitable habitat for the six oak species, with considerable variation in changes among species. We observed that the breadth of climate niche is related to the potential geographic distribution of the species and that the loss of area under future scenarios of global warming is significantly correlated with the climatic niche size. To keep pace with climate change, oak populations will need to colonize new areas, because a large part of their present ranges will not retain suitable climatic conditions. The oaks are dominant elements in the Mediterranean-climate region and pine-oak forests of the Baja California Peninsula, so changes in their distributions will probably affect other species that closely interact with them. Further studies on the demography and ecological interactions of these oaks are recommended to refine predictions concerning effects of climate change and to identify conservation management options.

1. Introduction

Climate conditions have changed drastically in recent decades as a result of the increase in emission of greenhouse gases into the atmosphere (IPCC, 2007). Faced with changing climate, species can adapt (reviewed by Hoffmann and Sgrò, 2011) or move to new areas with suitable climatic conditions (Walther et al., 2002). For example, over the end of the 20th Century, species were recorded moving to higher altitude and latitude (reviewed by Parmesan, 2006). The effect of global warming on the geographic distribution of a species is determined in part by the breadth of its climatic niche, which is described by the range of temperature and precipitation that allow species persistence (realized niche, Hutchinson, 1957). Geographically explicit predictions of climatic niches provide a good starting point for exploring regions with suitable climatic conditions for the species. Environmental Niche Models (ENMs) estimate the relationship between species records at sites and the environmental and/or spatial characteristics of those sites (Peterson and Soberón, 2012; Peterson, 2001). By projecting these models to future climatic scenarios, studies have assessed the potential

changes in the extension of suitable habitats for many species (e.g. Garza-López et al., 2016; Peterson et al., 2002; Thuiller et al., 2006).

Oaks (*Quercus*) are one of the most abundant and diverse groups of woody plants in the northern hemisphere (Nixon, 2006). Mexico is an important center of diversification for this genus, with 161 species in its territory, 109 of which are endemic (Hipp et al., 2017; Valencia, 2004). In the Baja California (BC) Peninsula, located in northwestern Mexico, 24 species of oaks have been recorded, including three endemics (Rebman et al., 2016). The BC Peninsula spans 10° of latitude, resulting in high climatic and habitat heterogeneity. In both extremes of this peninsula, there are extensive oak forests distributed in threatened biomes. In the North, oak forests occur across the Mediterranean-climate region, while in the South, they are dominant elements of the pine-oak forest and lowland deciduous forest of Sierra la Laguna (De La Luz et al., 2012). These biomes are suffering from accelerated changes of land use. For example, the Mediterranean-climate region has developed a high population density and great extent of urban area (Underwood et al., 2009). At the other end of the peninsula, large areas in Sierra la Laguna have been transformed to ranching (Lágu-

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Vázquez et al., 2013). The conversion of land use exacerbates the threat to biodiversity by climatic change (Klausmeyer and Shaw, 2009; Riordan and Rundel, 2014). It is necessary to assess how populations could respond to those threats to determine the susceptibility of species to extinction.

The effect of the future climatic change on endemic plants has been assessed in the North American mediterranean-climate region. In California, a change in the spatial extent and location of suitable habitat was predicted for several species (Conlisk et al., 2012; Kueppers et al., 2005; Loarie et al., 2008; Riordan and Rundel, 2014; Sork et al., 2010). For oaks that have a portion of their range in the BC Peninsula, the influence of climatic changes has been evaluated for the past (Last Maximum Glacial: e.g., *Q. chrysolepis*: Bemmels et al., 2016; Ortego et al., 2015) and the future (e.g. *Quercus engelmannii*: Conlisk et al., 2012). However, these previous studies did not show the present or predicted distributions in the BC Peninsula, being focused on California (e.g. Bemmels et al., 2016; Ortego et al., 2015) or because the study did not include locations from the Mexican portion of the range (e.g. May et al., 2009). Thus it is relevant to assess how those species, as well as endemics, might respond to future climatic change.

In this work, we evaluate the potential effects of two future climatic scenarios on the distribution of six species of oaks which occur in the BC Peninsula (*Q. agrifolia*, *Q. cedrosensis*, *Q. chrysolepis*, *Q. devia*, *Q. palmeri* and *Q. peninsularis*). We asked (i) How might climatic change affect the spatial extent of suitable area and what would the degree of overlap between current and future projections? (ii) Is the breadth of climatic niche related with the predicted future changes in the geographical distribution of the species? We chose these oaks because they occur in regions highly threatened by global warming (Mediterranean-climate and high-altitude forest; Loarie et al., 2008; Dirnbock et al., 2011), highlighting the necessity of assessing the vulnerability of these six species. In addition, the six oaks are extremely different in the size of their geographical ranges, which should allow us to assess whether the projected changes in area are related to the breadths of their climatic niches.

2. Material and methods

2.1. Study species, data collection, and climatic variables

We explored the climatic niches of six oak species occurring in the BC Peninsula; three also occur in the southwestern United States. Five of the species are found in the North American Mediterranean-climate region (*Quercus agrifolia*, *Q. cedrosensis*, *Q. chrysolepis*, *Q. palmeri*, and *Q. peninsularis*) and one is limited to the pine-oak forest (*Q. devia*) in the South of the BC Peninsula, in Sierra la Laguna (Figs. 1–S1).

For each species, we obtained georeferenced records from the Global Biodiversity Information Facility (GBIF, 2018a,b,c,d,e,f; www.gbif.org), Calflora data base (Calflora, 2018; <http://www.calflora.org/>), and the Flora of Baja California (BajaFlora, 2018; <http://bajaflores.org/>). The data were checked to remove duplicate records and corroborated using available information on species' altitudinal, latitudinal, and longitudinal distributions (Valencia, 2004; www.EFloras.org). To reduce possible autocorrelation bias due to local overrepresentation of records, we divided the sampling area for each species into cells of 1/10° and selected one point at random from each cell using the “raster” package (Hijmans, 2016), implemented in R v3.3.1 (R Core Team, 2016). The final dataset was reduced from 11,162 to 1869 records, which included 676 records for *Q. agrifolia*, 44 for *Q. cedrosensis*, 977 for *Q. chrysolepis*, 28 for *Q. devia*, 91 for *Q. palmeri*, and 53 for *Q. peninsularis* (Fig. S1, Table S1). The records encompass the reported distributions (Valencia, 2004; www.EFloras.org).

To describe the climatic niche and construct the ENMs, we used the bioclimatic variables layers (BIO1–BIO19, <http://worldclim.org/bioclim>; Hijmans et al., 2005), which include data on temperature, precipitation, and seasonality. To exclude highly correlated variables

that could bias subsequent analyses (McCormack et al., 2010), we extracted data from the 19 bioclimatic variables layers and conducted paired Pearson correlation tests, considering a > 0.75 threshold. From each pair of correlated variables, we excluded the one that had more than one significant correlation with another variable. Using these criteria, we retained 11 bioclimatic variables, as follows: BIO1 (annual mean temperature), BIO2 (mean diurnal range), BIO8 (mean temperature of wettest quarter), BIO9 (mean temperature of driest quarter), BIO12 (annual precipitation), BIO13 (precipitation of wettest month), BIO15 (precipitation seasonality), BIO16 (precipitation of wettest quarter), BIO17 (precipitation of driest quarter), and BIO18 (precipitation of warmest quarter).

2.2. Environmental niche models and climatic niche

To define the size of the geographic mask used to build the current model and future projections of the six species, we used the following procedure: We generated (i) species-specific masks that included the species' records and extended 200 km beyond, and (ii) an all-species mask that included the records of the six species and an extension of 200 km. Next, for each species, two MAXENT models were run to obtain the projected distribution, using the 11 environmental variables for present climate; one model used the species-specific mask, and the other used the all-species mask. The area of projected distribution was calculated for both models, and we found that the projections using the species-specific and all-species masks were extremely similar. For further study we selected the mask that included the records of all six species because this mask represents a greater environmental variability and allows comparison between species under the different global warming scenarios considered.

ENMs were built using the selected set of 11 bioclimatic variables. For the case of the future climate, we used the representative concentration pathways (RCPs; Moss et al., 2008) for 2070 (i.e. the average among years 2061–2080) based on the Community Climate System Model 4 (CCSM4; Gent et al., 2011). These models were generated from the Coupled Model Intercomparison Project Phase 5 (CMIP5, <https://pcmdi.llnl.gov/?cmip5/>), and they are available from the WorldClim database (www.worldclim.org). To evaluate different climate change scenarios, we used RCP8.5 (Riahi et al., 2007) which predicts the highest increase in global temperatures, and the more conservative RCP4.5 (Wise et al., 2009) which predicts less temperature increase.

The current models and future projections were generated using the “biomod2” v 3.1 platform (Thuiller et al., 2016) implemented in R. The final models were constructed using the committee-averaging criteria by means of creating ensemble models (Araújo and New, 2007; Qiao et al., 2015). For these ensembles, seven modeling algorithms were computed, as follows: the generalized linear model (GLM; McCullagh and Nelder, 1989), generalized additive model (GAM; Hastie and Tibshirani, 1990), generalized boosted model (GBM; Friedman, 2001), artificial neural networks (ANNs), random forest (RF; Breiman, 2001), multivariate adaptive regression splines (MARS; Friedman, 1991), and MAXENT (Phillips et al., 2006). For each computed algorithm, two independent pseudo-absence sets of 5000 points were generated at random using the previously created mask. For each species, five random replicates were run, using 70% of the records to train the modeling and 30% to evaluate the performance. In total, 70 models (seven algorithms, two pseudo-absence sets, and five random replicates) were run per species to obtain the final ensembles. We assessed model performance using the area under the receiver operating characteristic curve (AUC; Swets, 1988) and true skill statistic (TSS; Allouche et al., 2006). The ensemble computation was restricted to models with AUC > 0.9 and TSS > 0.8. The algorithm performance is influenced by the number of presences, spatially autocorrelated presences, and pseudo-absence points (Barbet-Massin et al., 2012). However, our evaluation criteria were stricter than the commonly used ones; in this sense, we are confident that the bias was minimized. The final

ensembles were transformed to presence/absence values (binary transformation) selecting the threshold that maximized the specificity and sensitivity (i.e., the TSS score).

To evaluate the potential effect of future climate change on the geographic distribution of oak species, we estimated the change in the extent of the geographical range and the degree of overlap between current and future distributions. For the first estimation, we computed the area in square kilometers for the binary projections of current time and future scenarios using the “area” function of the R package “raster”. We then calculated the relative change in the area as $(FP - PT)/PT$, where FP is the predicted area in square kilometers of future projection, and PT is the predicted area of current time. A zero value of this ratio indicates no change in the extent of predicted range; a positive value indicates an increase, while a negative value shows shrinkage in the spatial extent of the distribution. To assess the degree of overlap between current and future projections, we created three categories according to the differences in the geographic area projected between the current time and future scenarios, as follows: Shift, Conserved, and Highly Conserved. The “Shift” category refers to any change in the distribution area between the current time and at least one future scenario (i.e., total area predicted for the future but not in the present). The category “Conserved” refers to total area for which at least one future scenario overlaps with the current time model. Finally, the “Highly Conserved” category refers to total area of overlap among the current time model and both future scenarios. It should be noted that, for this analysis, we included both future scenarios at the same time (RCP4.5, RCP8.5).

To test the relationship between the area of distribution (square kilometers) and the climatic niche breadth, we calculated the latter as the volume of a Minimum Volume Ellipsoid (MVE; Van Aelst and Rousseeuw, 2009) in the NicheA v3.0 software (Qiao et al., 2016). We extracted climatic data from the 11 bioclimatic variables previously used for the ENMs, and performed a principal components analysis (PCA). Using the first three axes, we created the environmental background, yielding more than 2 million points. The climatic niche breadth (MVE) of each species was generated using the current time's binary model. We used Pearson correlation to test whether the climatic niche breadth (volume) was related to the area of current distribution (square kilometers) and to the decrease of the predicted area in each future scenario. We used JMP software to run the statistical analyses.

3. Results

All Environmental Niche Models had high predictive power (TSS > 0.8 and AUC > 0.9), and the MAXENT algorithm showed the highest performance (Table S2). The most relevant bioclimatic variable predicting the current distribution varied among species (Fig. S2), but BIO17 (precipitation of driest quarter), BIO8 (mean temperature of wettest quarter), and BIO15 (precipitation seasonality) were important across all species. *Quercus palmeri* and *Q. agrifolia* had the widest distributions, while *Q. devia* was the most restricted. *Quercus peninsularis* and *Q. agrifolia* had unfragmented predicted distributions, while *Q. cedrosensis*, *Q. palmeri*, and *Q. chrysolepis* were highly fragmented (Fig. 1).

The projections to the future scenarios indicated that all species are likely to undergo changes in the extent of their geographic range (Figs. 1, 2). For both future scenarios, *Q. peninsularis*, *Q. cedrosensis*, and *Q. chrysolepis* were predicted to lose more than 12% of suitable habitat, and *Q. devia* was predicted to lose more than 95% of suitable habitat. Meanwhile, *Q. palmeri* showed an increase of 9% in RCP8.5 and a reduction of 3% in RCP4.5 (Fig. 2), and *Q. agrifolia* showed increases of 7% and 16% for RCP4.5 and RCP8.5, respectively.

The degree of overlap between the current time and future projections also exhibited differences among species (Fig. 1). All species showed a reduction in terms of highly conserved areas. For *Q. devia*, *Q. cedrosensis*, and *Q. peninsularis*, the highly conserved areas were less

than half that in the current time (they are situated in the bottom-left quadrant of Fig. 3), while *Q. chrysolepis* despite its loss of area, retained more than 50% of the current distribution (it is situated in the bottom-right quadrant of Fig. 3). *Quercus agrifolia* is the least affected species, with future predictions showing a gain of area and the greatest retention of highly conserved area (it is situated in the upper-right quadrant of Fig. 3).

Regarding the oaks' climatic niches, we observed that the ellipsoid volumes were highly variable (Fig. 4, Table S3). *Quercus palmeri* had the broadest climatic niche, while *Q. devia* had the narrowest. There was a high overlap among climatic niches in terms of the environmental space occupied by the species (Fig. 4, Table S3). *Quercus palmeri*'s climatic niche contained almost the entire climatic niche space of *Q. chrysolepis*, *Q. peninsularis*, *Q. cedrosensis*, and *Q. agrifolia*, and a small part of *Q. devia* (Fig. 4). The PCA of raw GIS data indicated three main niche axes that together explained 85% of the variation (Table S4). The first niche axis was associated with annual precipitation and precipitation of the wettest months. The second niche axis was associated with rain seasonality, while the third niche axis was associated with rain in the warmest quarter.

We found a significant positive correlation ($R^2 = 0.693$, $p = 0.024$) between the breadth of climatic niche (ellipsoid volume) and the size of the current distribution of the species. Thus, for the studied oaks, broader climatic niches tend to be associated wider geographic distribution. We also observed a significant negative correlation between the breadth of climatic niche and the predicted loss of suitable area under both future scenarios (RCP4.5: $R^2 = 0.666$, $p = 0.029$; RCP8.5: $R^2 = 0.709$, $p = 0.022$), indicating that those species with a narrower climatic niche, will lose relatively more suitable area.

4. Discussion

This is the first study to evaluate the possible impact of global warming on oak species distributed in the Baja California (BC) Peninsula, Mexico. We found that climate change will modify the location and spatial extent of suitable habitat for six oak species, with considerable variation in responses among species. Models were fairly accurate (AUCs > 0.9) for current distributions, and showed differences among habitat preferences and extents: *Quercus devia* is restricted to the mountains of Sierra de la Laguna in the southern peninsula, while the other species occur across the northern region (*Q. cedrosensis*, and *Q. peninsularis*) and also the entire California Floristic Province (*Q. chrysolepis*, *Q. agrifolia*, *Q. palmeri*). Contiguous areas are predicted for *Q. peninsularis* and *Q. agrifolia*, and fragmented areas are predicted for *Q. cedrosensis*, *Q. palmeri*, and *Q. chrysolepis*. Habitat fragmentation, in addition to the direct effect of global warming, may increase the risk of extinction for oak populations, considering that they have low rates of seed dispersal (Vander Wall, 2001). In addition, fragmented landscapes may have less successful seedling establishment, and thus lower recruitment and lower foundation of new populations, due to negative effect of external factors on microsite conditions (Perea et al., 2011).

The variation observed among geographical ranges of species probably results from different life history characteristics, ecological factors, and evolutionary processes. Variability in geographical ranges among closely related taxa has already been explored (e.g. Gregory and Gaston, 2000; Lester et al., 2007; Webb and Gaston, 2000) with no single characteristic robustly describing species distributions (Lester et al., 2007), but rather a set of factors strongly mediating the size of geographical ranges (e.g. Laube et al., 2013). It is interesting to note that the MVEs overlap extensively, except for *Q. devia*. Some of the environmental variables with greater predictive power in our ecological niche models were the same among species, specifically, those that describe drought (e.g. precipitation of the driest quarter, precipitation seasonality). Additionally, the variables associated with the first three niche axes in the NicheA analysis, were also associated with precipitation, indicating that the latter are main descriptors of the oaks'

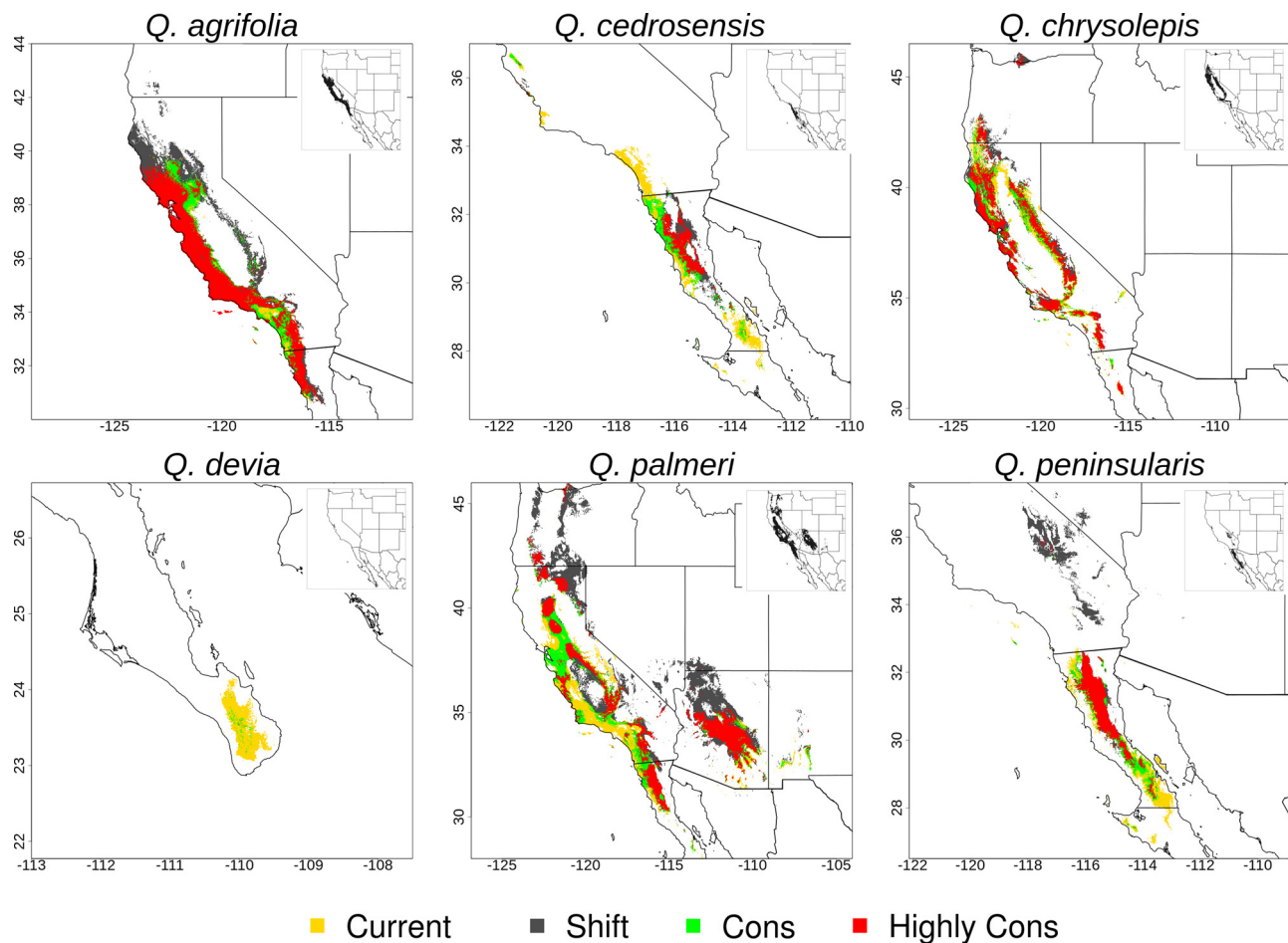


Fig. 1. Environmental Niche Models (ENMs) for the six *Quercus* species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

“Current” (yellow color) refers to the area predicted in the current time but not in the future. “Shift” (gray color) refers to area predicted in at least one future scenario but not in the current time. “Cons” (green color) refers to areas where at least one future scenario overlaps with the current time, and “Highly Cons” (red color) refers to areas that overlap among the current time and both future scenarios.

climatic niche. Both results suggest that there are characteristics, probably related to drought stress, conserved among these phylogenetically close entities. The summer is the driest season in the North American Mediterranean-climate region, and plants need to avoid or tolerate drought stress to survive. In this way, summer drought is probably an important condition that limits the habitat suitability for these species. Our findings fit with a previous report that highlighted the importance of drought in the historical change of the geographic range of *Q. chrysolepis* on California Floristic Province (Bemmels et al., 2016).

Tolerance to a wide range of climatic conditions facilitates the occupation of larger geographic areas (Slatyer et al., 2013). The results of our study support this pattern, as we found a positive relationship between range size and niche breadth. The species with the widest climatic niche was *Q. palmeri*, and it has the largest range (Figs. 1, 4), while *Q. devia*, has the narrowest niche breadth and the smallest range. The tolerance to a wide range of climatic conditions also could influence the effect of climatic change on the geographic distribution of a species, as we found. The loss of habitat under future climate change scenarios was significantly correlated with climate niche breadth. For species with a narrower niche, the spatial extent of suitable habitat was predicted to be much lower in the future than now. Restricted-range species are predicted to be more vulnerable to global warming (Urban, 2015), because many of these species are habitat specialists (e.g. Dirnböck et al., 2011) and changes in the spatial extent and location of suitable conditions can dramatically reduce their distributions. On the

other hand, species with wider climatic niches probably will have higher chances of finding suitable habitats in the future time because they are more tolerant to a wide range of environmental conditions.

For five of the six oak species studied, under one or both climate scenarios, suitable habitat was predicted to decline, similar to previous reports for other plants (Garza-López et al., 2016; Sáenz-Romero et al., 2015). The most affected species was the peninsular endemic *Quercus devia*. Future projections show a dramatic reduction in the spatial extent of its suitable area. It is likely that the fate of *Q. devia* is similar to the future of many plant communities of this mountain range, which contains the highest level of endemic species in peninsula (Ortega-Rubio et al., 2012). At the global level, a large impact has been predicted on taxa distributed in mountainous areas and with affinities to relatively cooler conditions (Parmesan, 2006; Walther et al., 2002). At the regional level, this pattern has already been reported in plants already found only on the highest mountains of central Mexico (Gutiérrez and Trejo, 2014).

Comparing the two global warming scenarios, we found considerable variation in responses among species. The most extreme scenario is predicted to cause habitat loss in four of the six species. Meanwhile, the moderate scenario may cause some habitat gain for *Q. agrifolia* and mitigate habitat loss for *Q. cedrosensis*. Previous studies reported different effects of the climatic change over the geographic distribution of oaks from the North American Mediterranean-climate region. For example, a reduction has been predicted for *Q. engelmanni* under future scenarios of drier climates (Conlisk et al., 2012), while contrasting

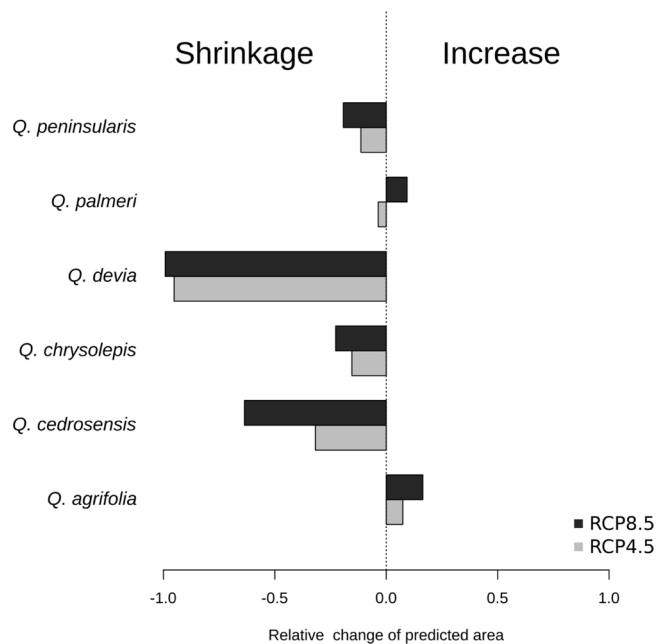


Fig. 2. Change of projected area in square kilometers relative to current time for the six studied *Quercus* species, under the conservative RCP4.5 and the extreme RCP8.5 models. A negative value indicates a decrease in the predicted area of distribution, and a positive value indicates an increase in the predicted area of distribution.

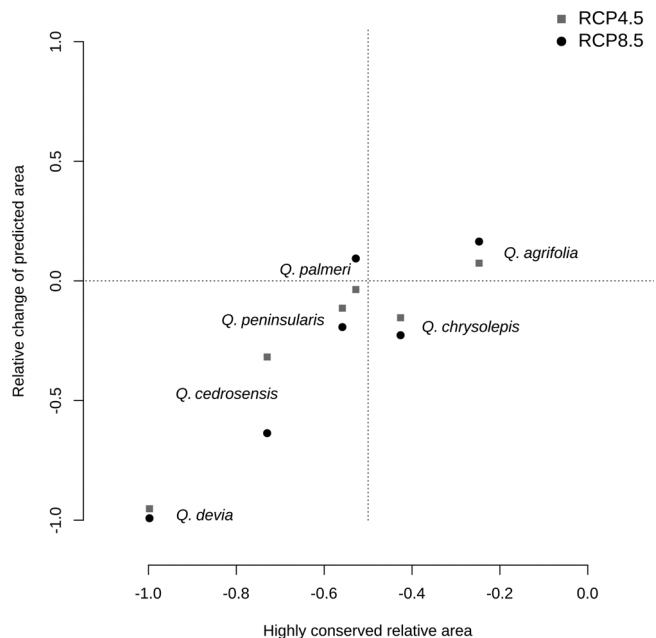


Fig. 3. Plot of the highly conserved area vs the relative change of predicted area in the future. Points left of the vertical dashed line indicate future predictions with less than 50% of highly conserved area relative to the current time. Points above the horizontal dashed line indicate an increase in the predicted area; points below indicate a decrease in the predicted area. RCP4.5 and RCP8.5 are the conservative and the extreme models.

regional outcomes were detected for the geographic distribution of *Q. lobata* (Sork et al., 2010). In addition, the warming since the last glacial period has caused a progressive isolation and fragmentation of *Q. palmeri* (May et al., 2009) and *Q. chrysolepis* populations (Bemmels et al., 2016; Ortego et al., 2015); we found similar results for these species on the timescale of only a few decades.

Global warming will shift the range of the six studied species. In the

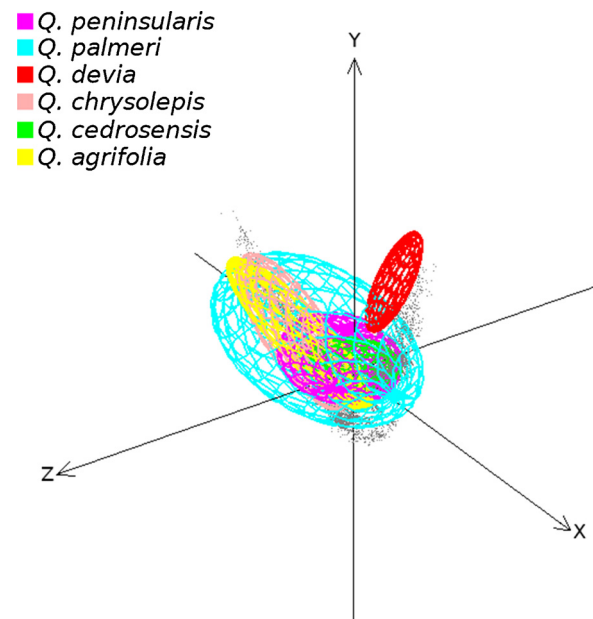


Fig. 4. Breadth of the climatic niches of the six *Quercus* (represented as Minimum Volume Ellipsoids). Gray dots represent the environmental background produced by the Principal Components Analysis (PCA) of the 11 selected variables. The size and shape of the climatic niches are shown in the three-dimensional visualization of the first three principal components. Plot produced by NicheA.

future scenarios, we detected changes in the extent and position of areas with suitable conditions. This pattern of available areas in the future in regions other than current ones has been registered for other plant species in the California Floristic Province (Loarie et al., 2008), and implies that in a short time plant populations need to colonize new areas to remain within the set of suitable climatic conditions. If we consider the low vagility of the oaks and rapid climate change, it is unlikely that many species will be able to keep pace (McLachlan et al., 2005; Pearson, 2006). Our results demonstrate that global warming favors a new combination of species along the landscape, modifying plant communities and generating new patterns of ecological interactions (Loarie et al., 2008).

5. Conclusions

Global warming will have contrasting effects on the geographic distribution of the six oak species we studied. In the future, a large part of the ranges they currently occupy will not retain the set of climatic conditions suitable for their presence. The description of the climatic niche is a valuable tool for predicting effects of global warming, because the loss of area in the future projection was negatively correlated with the breadth of the niche of the species.

The effects of climatic change on the geographic distribution of species will be the result of different process occurring at the edges of their ranges. Some populations may be expanding because new areas with suitable climatic conditions are available (high-latitude margins), and dispersal events, followed by exponential population growth, drive the colonization front. Meanwhile, at the southern margins of the ranges (the low-latitude limit), other populations are losing suitable climate and could become extirpated (Hampe and Petit, 2005; Thuiller et al., 2008). The short-term responses of plant populations to climatic change partially depend on species' life history traits, such as generation time and reproductive rates (Thuiller et al., 2008). Phenotypic plasticity is also an important feature because it allows a species to maintain a viable population (Ghalambor et al., 2007). Finally, biotic factors like ecological interactions will influence changes in their

geographic range, since the populations will be able to persist where they can interact with others organisms that facilitate their growth. Further studies on the demography and ecological interactions of these oaks are recommended to strengthen the climate niche predictions with new dimensions.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.flora.2018.12.006>.

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